CLUTCH SIZE IN KITTIWAKES *(RISSA TRIDACTYLA)* ON LUNDY

by
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ABSTRACT

Kittiwake *(Rissa tridactyla)* numbers on Lundy have been in decline for many decades. This decline is monitored using occupied nest counts and productivity data. More recently we have begun collecting data on clutch size at one colony on Lundy. Clutch size is a direct response by a bird to prevailing conditions. Therefore, clutch size data is potentially revealing in terms of what it tells us about Kittiwake response to factors such as food availability and predation risk, in a way that occupied nest counts and productivity data is not. Calculating clutch size is not straightforward for a colonial cliff nesting bird. In this paper we present a pilot study that has calculated clutch size, and then use that data to assess differences in clutch size across the colony with reference to possible differences in predation risk as a function of colony structure. We discuss the limitations of this pilot and also key aspects of the broader ecology, which we believe should also be monitored in order to better understand the plight of this seabird.

INTRODUCTION

There is much research investigating Kittiwake (*Rissa tridactyla*) decline in the north of the United Kingdom (U.K.) and in particular the North Sea. Far less work has been conducted on southern populations (McMurdo Hamilton *et al*. 2016).

We have begun monitoring a colony on Lundy in order to address this issue, but also to pilot the collection of reliable clutch size data. In this paper we present pilot data, discuss the methods involved, and test to see if differences in clutch size are related to key aspects of colony structure that may increase or reduce threats to breeding success. We also make comment on predation and food webs in the context of a broader discussion about key ecological factors.

CLUTCH SIZE

As a direct investment in fitness, the causes and consequences of clutch size variation have been much studied (Ricklefs 2000; Stearns 1992; Winkler & Walters 1983). Clutch size varies within and between species; but females in a given species can be said to produce a modal number of eggs.

Lack assumed that the key factor influencing clutch size is food availability; natural selection acted to set clutch size at a value that can be supported by background food resource (Lack 1947). This hypothesis was modified to include foraging effort and

maintenance (Cody 1966) and the costs of reproduction associated with larger broods (Ricklefs 1970), but at root it was food availability that was seen as the principal factor. As Ricklefs (1970) pointed out, the food web dynamics, incorporating predator-prey interactions, may help to account for variation in clutch size. For example, clutch size is lower nearer to the equator, possibly as a consequence of higher rates of inter-specific competition for prey items. This would impact upon functional prey abundance. This view sees clutch size as responsive to local ecological parameters, within limits set by natural selection.

Lack's hypothesis was applied to all birds without consideration of life-history differences (Winkler & Walters 1983) and his sole concern was with the optimum number of offspring that resource would allow. Life-history theory has since been incorporated, using individual fitness maximization as the modelling assumption, and allowing consideration of trade-offs between current and future reproductive effort, and quality and quantity of offspring (Stearns 1992). The longevity, and developmental trajectory of birds will introduce different solutions to these trade-offs; and longevity and development are themselves subject to natural selection and niche specialization (Winkler & Walters 1983). Some of these solutions will be plastic, in response to local ecological variation, and will be optimal solutions (Stearns 2000)

Nest predation has also been hypothesized as a factor in reducing laid clutch size. Larger clutches may take longer to process, and thus increase exposure to predators; predators may more readily detect larger broods; and, smaller clutches make the production of a replacement clutch easier, due to 'saved resource', or increase parent survival chances across more than one breeding season (Julliard *et al*. 1997).

It is clear that clutch size is sensitive to ecological variables. Variation in clutch size is a direct response to conditions in the recent past and present breeding season; a response based on the information processing capacities of the birds themselves. Various mathematical models allow clutch size data to predict the number of fledglings produced, assuming no predation (Stearns 1992) which would allow estimates of fledging success to be more accurate following productivity surveying. In essence, a shortfall could be accurately calculated that was sensitive to the adult birds' reproductive decision each season. Given this, clutch size data should be of great use in the monitoring of species of conservation concern, alongside the more usual data on apparently occupied nests and productivity (Bibby *et al*. 2000).

THE KITTIWAKE

The Kittiwake is the most common gull worldwide, found in both the North Atlantic and North Pacific oceans. Kittiwakes are a long-lived species, with some birds living 28 years or more. They are a seasonal breeder, returning to the coast in the late winter and beginning their breeding effort in April (Coulson 2011). They have low levels of philopatry, recruitment relying upon immigration, and high levels of nest site loyalty (Coulson & Coulson 2008). Kittiwakes are highly monogamous, with a 25% divorce rate and an 11% partner mortality rate per annum. Divorce is associated with poor breeding success the previous year (Coulson 1966).

Kittiwakes are a nidicolous species, with chicks in need of adult care for food up until fledging and thermoregulation during the early days post hatching. Most models of

clutch size discussed above rely upon altricial, or nidicolous, species whose young put demands upon their parents. These demands yield specific life-history trade-offs. In a long-lived species, those trade-offs can span across future generations leading to sabbatical years in breeding and calibration of breeding effort in part through control of clutch size (Erikstad *et al*. 1998; Stearns 1992).

Clutch size varies from one to three eggs, with the mean clutch size slightly below two-eggs, and more one-egg clutches than three (Coulson, 2011). Average clutch size can vary annually in some regions, whilst remaining stable in others. Clutch size is possibly related to individual quality and also breeding experience, with inexperienced breeders producing more eggs (Coulson & Porter 1985). It is also possible that clutches of more than one egg are a bet-hedging response, such that the beta chick in this asynchronously hatching species is an insurance policy against the loss of an alpha chick. Such a strategy should be sensitive to local conditions and may lead to the emergence of obligate siblicide (Anderson & Ricklefs 1992; Dickins & Clark 1987). Experimental evidence suggests that Kittiwakes produce optimal clutch sizes that match the number of young they can successfully fledge (Jacobsen *et al*. 1995).

The status of the Kittiwake

In the U.K., Kittiwakes are red-listed due to a 40% decline in breeding populations between 1969 and 2008 (Eaton *et al*. 2015; JNCC 2009). Food availability has been linked to colony success, especially in northern populations (Coulson *et al*. 1985; McMurdo Hamilton *et al*. 2016). During the breeding season, year-zero sand-eels *(Ammodytidae)* are the principal source of food for adults and their chicks. Sand-eels prefer cold winters to spawn (Frederiksen *et al*. 2004) and climate change has affected sand-eel recruitment, in turn affecting Kittiwakes (Frederiksen *et al*. 2005). It is possible that food availability impacts upon adult survival rather than breeding effort (Oro & Furness 2002). There is also evidence that commercial fisheries, marine contaminants, introduced species and visual disturbance to the marine environment are all contributing to a widespread decline in seabird populations (JNCC 2009). Few data are available on clutch size effects but, in one study, Hamer and colleagues found that it was not affected by food availability. Instead, food availability appeared to impact upon fledging success (Hamer *et al*. 1993).

Populations on Lundy have declined over many years, with many colonies collapsing (Davis & Jones 2007; Price *et al*. 2013). Records began in 1939 when there were 3,000 occupied nests. 1950 saw the next complete survey, when there were 1,387 occupied nests. From 1950 to 1973 11 surveys were undertaken and the numbers peaked at 2,026 and dropped to 718. From 1981 (933 occupied nests; Figure 1) there has been a steady decline, to a population of 127 occupied nests (Price *et al*. 2013).

Wardens have undertaken productivity surveys on the island since 2007, going beyond nest occupancy data. The data have been published for the current field site (Figure 2a,b) (Saunders 2008; Wheatley 2011; Wheatley & Saunders 2010; Brown *et al*. 2011; MacDonald 2014).

Whilst food resource may be an issue, so is predation risk. Avian predators will take eggs and chicks at the nest, and adults in flight. Key predators, such as Great Black-backed Gulls (*Larus marinus*) and Peregrines (*Falco peregrinus*) have thrived in recent years (Davis & Jones 2007).

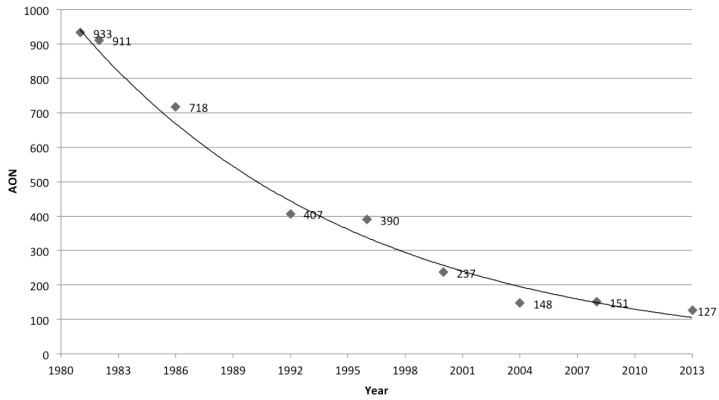

Figure 1: Declining Kittiwake numbers (unit: apparently occupied nests, AON) on Lundy over nine surveys from 1981 to 2013, with exponential fitted ($y=6E+61e^{-0.068x}$)

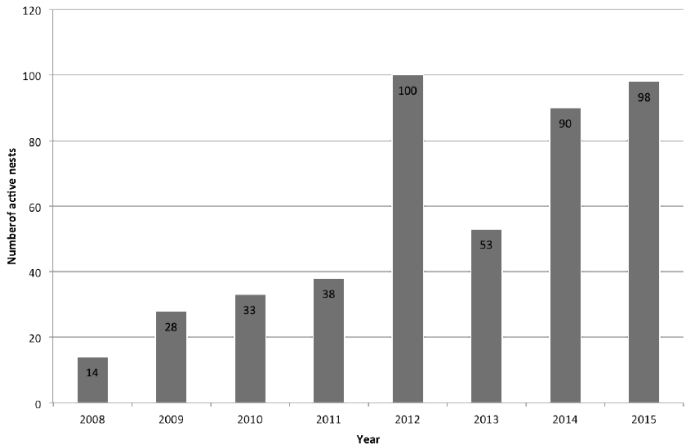

Figure 2a: Number of active nests for the Aztec Zawn colony across eight years. Data for 2012, 2014 and 2015 provided directly by Beccy MacDonald (Warden); all else sourced from JNCC: http://jncc.defra.gov.uk/smp/ and publications cited

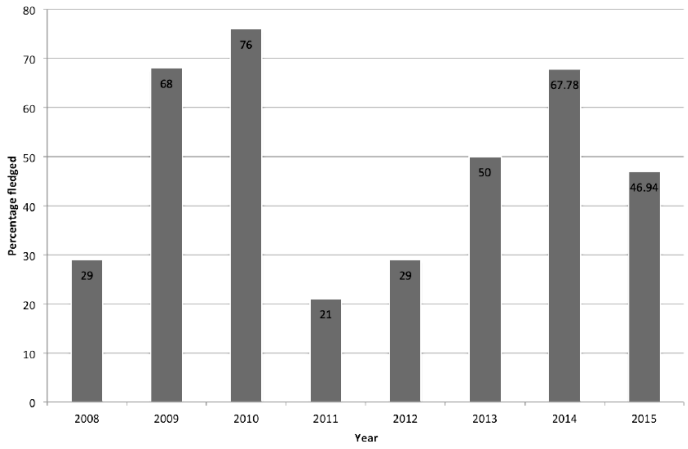

Figure 2b: Kittiwake breeding success data for the Aztec Zawn colony across eight years. Success is the number of birds fledged per active nest site, expressed as a percentage. Data for 2012, 2014 and 2015 provided directly by Beccy MacDonald (Warden); all else sourced from JNCC: http://jncc.defra.gov.uk/smp/ and publications cited

COLONIAL NESTING

Colonial nesting provides group defence, which can deter predators. Colony-level hatching synchrony reduces the chances that an individual egg or chick is predated (Birkhead 1977). Benefits may also accrue in foraging: mass feeding on fish schools will disrupt fish defences, but also information about foraging sites is possibly shared (Clode 1993).

Kittiwakes nest on narrow ledges on sea-cliffs (Coulson 2011; Cullen 1957; Danchin & Nelson 1991), and occasionally on buildings (Coulson *et al*. 1985). Naturally occurring sites can be on broad, exposed cliff faces, or within narrow gullies and inlets. Kittiwakes often share ledges with Guillemots *(Uria aalge)* in the U.K. and other auk species elsewhere. Nesting density, ledge accessibility and wind conditions have all been shown to correlate with predation rates of auks by *Laridae* (Birkhead 1977; Gaston & Nettleship 1981; Gilchrist *et al*. 1998).

Kittiwake eggs and chicks are commonly predated by large gulls, including Herring gulls *(Larus argentatus)* and Great Black-backed gulls, and corvid species (Coulson 2011; Dixon 1979). Peregrine falcons also take chicks at night (Collins *et al*. 2014) and will take adults in flight (Hipfner *et al*. 2011). Hipfner and colleagues demonstrate that the presence of Peregrines deters other predators, thereby reducing the overall predation rate on Kittiwakes. A similar hypothesis has been mooted for the relationship between Guillemots and *Laridae* on Lundy (Davis & Jones 2007), such that territorial gulls nesting nearby would chase off other gulls and corvids, thereby reducing the overall predation rate. It is possible this may extend to Kittiwakes given the close proximity of their nesting to territorial Great Black-backed gulls.

Kittiwakes rarely raise an alarm call and they allow predators to approach much closer than a ground nesting bird would (Cullen 1957) prior to taking flight. Kittiwakes rarely attack predators, although intense predation may lead to greater defence (Massaro *et al*. 2001). According to Cullen, it is the inaccessibility of the nest sites that is the main defence.

Nest sites will vary individually with respect to ledge structure, position in the colony, and therefore accessibility to predators, such that variation in predation rates within colonies should be expected (Aebischer & Coulson 1990; Massaro *et al*. 2001; Regehr *et al*. 1998). Aebischer and Coulson (1990) demonstrated that there was no difference in mortality risk for adults nesting in the centre of the colony, compared with the periphery. However, peripheral nesters had a higher rate of mortality at sea in the winter months, possibly indicating some fitness differential across the colony. There was no evidence of increased egg and chick loss at the periphery of colonies, relative to the centre. The colonies used in this work were under very low predation risk (Regehr *et al*. 1998).

Regehr and colleagues (1998) studied populations under very high predation rates. The predators were Great Black-backed gulls, Herring gulls and Ravens *(Corvus corax)*, all under food stress, and they took 90% of Kittiwake eggs in each year of a two-year study. This is exceptionally high, the authors citing a 5% loss, mostly to Ravens, when other prey items were abundant in previous years. Regehr *et al*. found that productivity was 'highest on sheer cliffs, and lowest on irregular and less steep cliffs' (p.913), indicating that access was important to predators. Great Black-backed gulls found landing on more regular, steep cliff structures more difficult; overhangs above nests reduced predator access and led to higher productivity. In the second year of the study a central position in the colony predicted productivity.

The central portion of a colony is that which is settled first during annual recruitment (Coulson 2011) and is not related to the topography of the site. However, if Aebischer and Coulson (1990) are correct, and centrally nesting birds are of higher quality in some way, it is possible that these are more dominant birds that are actively choosing a safer set of nest sites. Regehr *et al*. (1998) have partially supported the idea of a central benefit to productivity, and this may simply be a consequence of reduced ease of access and increased group defence. However, this effect was only found during one year. It is also of note that birds settling the centre of a colony tend to be older and have arrived at the coast earlier (Coulson, 2011). It is possible that this population is larger, and aggregates more densely enabling reduced predation risk and higher productivity at times.

Nests in areas of high and medium nesting density were twice as likely to be attacked as nests in low density areas (Massaro *et al*. 2001). However, high-density nests had greater breeding success, in part due to observed greater recruitment to group mobbing in these zones. The upper sections of the cliffs were more likely to be attacked than lower sections, but there were no breeding success differences between upper and lower. Nests on narrow ledges had higher breeding success than those on wider. When there were high winds Herring gulls seemed able to land on a greater variety of positions, increasing their opportunities (Gilchrist *et al*. 1998).

RESEARCH OBJECTIVES

In June 2015 clutch size data was collected at the current study colony. During that period, informal observations indicated that gull predation was a regular occurrence (Dickins 2016). However, the colony did not appear under intense predation at this time; Figure 2b displays a 47% fledgling success rate. Given these observations, a systematic method was planned for piloting in 2016, the aims of which were:

1. To describe the colony in terms of physical nest site characteristics following Massaro *et al*. (2001);
2. To calculate the daily rate of predation attempts and map the sites of those attempts with reference to 1;
3. To collect data on clutch size and determine if there is an association between clutch size and physical nest site characteristics.

The underlying assumption is that certain nests are more vulnerable to predation and this could be reflected in different clutch size decisions, following Julliard *et al*. (1997).

METHODS

Field site

The colony is on a south-facing cliff (Figure 3) of a narrow gully, north of St Mark's Stone. An established observation site was adopted (51.18719° N, 4.6747° W) on a promontory 116m south of the colony, and 54m above sea level (asl). This elevation enabled observers to look down on the colony, which extends to approximately 45m asl (Bibby *et al*. 2000). Three observers (TD, KN and RS) took turns (independently) to collect data at this site from 6-17 June 2016. This is the late incubation period for Kittiwakes, which is the recommended time window for survey work (Bibby *et al*. 2000).

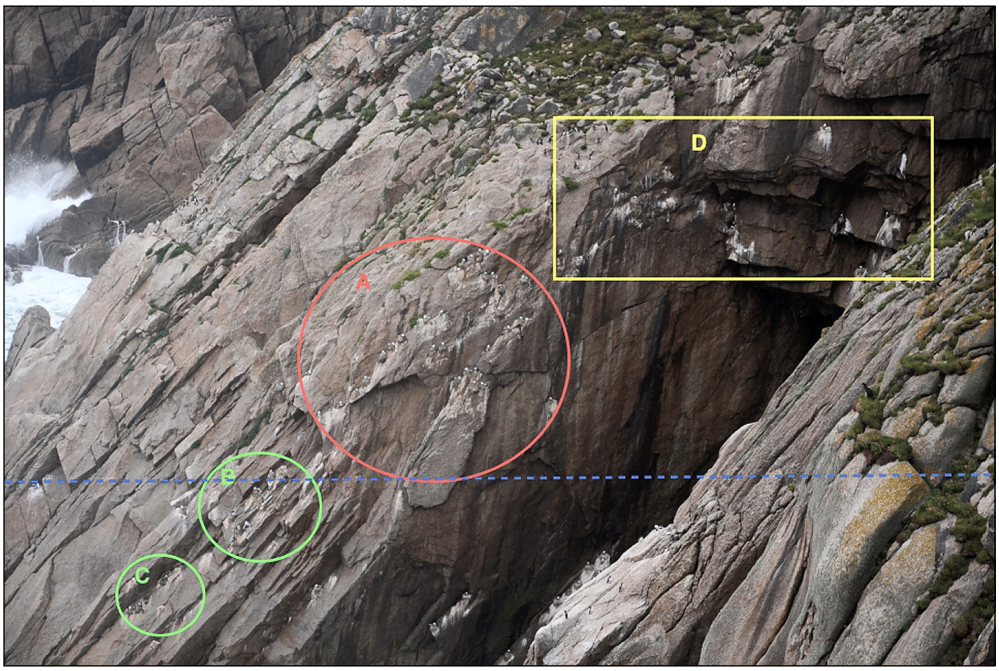

Figure 3: Photographic map of the Aztec Zawn colony with regions marked out, and a dotted line dividing the upper and lower portion of the colony (see main text for details). © Tom Dickins, 2016

Procedure

Hand drawn maps of the colony were produced, and a nest number system agreed. The map relied upon a few distinctive geological features and the clustering patterns of the sites. This minimal approach reduces confusion when the colony is viewed from differing angles. The maps were found to accord with photographic images taken in 2015 and 2016 (Bibby *et al*. 2000).

Table 1: RSPB bird monitoring codes for a Kittiwake survey

Code	Description
I	Apparently incubating adult
c/n	Clutch of n eggs
c/0	Empty, well built nest with adult in attendance
c/x	Well built nest with adult standing, contents unknown

A daily census sweep was made to assess the status of the colony using standard codes (see Table 1; (Gilbert *et al*. 2011)) to count the number of incubating adults and to gain some knowledge of nest contents. Apparently occupied nests (AON) are the main census unit for seabird monitoring (JNCC 2009) but this method is prone to overestimate breeding success as Kittiwakes will occupy nests and not lay (Bibby *et al*. 2000; Walsh *et al*. 1995). Whilst the standard codes record contents a typical census will not have time to systematically collect contents data and so AON data is most

commonly reported. None the less, this information usefully describes the activity of the colony and enables an upper estimate of possible productivity to be calculated. Final counts should be the mean of at least three AON counts (Bibby *et al*. 2000).

Once the census was completed, a direct count opportunity sampling method was undertaken each day, to collect more detailed data on clutch size. Opportunity sampling involved visually scanning the colony for movement of adults at the nest and then using binoculars, or more powerful optical equipment, in order to yield an egg or chick count for each nest. For example, when an adult stood up from an apparently incubating position this would provide an opportunity to inspect the nest contents. The colony was regularly scanned with binoculars to assess movement. On occasion data were gathered during the initial census sweep if adults were moving on the nest.

Whilst the direct count methods yields more detail it is not the case that perfect information is collated about colony clutch size. All surveys are time-limited and during observation periods some adults do not move from their nest. This leads to missing data (see below).

This survey work commenced at different times of day and under varied weather conditions (Table 2) and used standardized sheets.

Colony and nest characteristics

Figure 3 displays a zoning system applied to the colony, after all the data were collected. Zones A-D represent distinct clusters of AON. All other AON that are not clustered were allocated to zone E. This clustering is subjective but that subjective perception could introduce biases into data collection and so warranted analysis.

Figure 3 shows a line demarcating the colony into the upper and lower regions (Massaro *et al*. 2001). All previous predation attempts witnessed by the first author occurred above this line.

Each nest was photographed using a telephoto lens and these images were used to characterise nesting ledges once back from the field (following (Gaston & Nettleship 1981)). Ledges were categorized as narrow if nest material hung over the seaward side, wide if there was clear space between the nest and the edge of the ledge, and medium if the nest fitted snugly, with no overlap, onto the ledge. The number of vertical walls, more than twice the height of a sitting adult at the nest, was counted. A nest might be on a ledge directly abutting the cliff face, thereby having one vertical wall only; but nests may also be in a corner (two vertical walls) or in a more complex niche with three or more vertical walls. A nest was considered to have a roof if rock protruded over the nest, covering the whole cup, within twice the height of an adult Kittiwake.

The number of neighbouring nests for each nest was calculated. A neighbouring nest had to be within pecking distance of the focal nest. Pecking distance only included pecking that occurred/might occur between adults seated on their nests. This was estimated, based on observations from 2015 and 2016. All neighbour disputes were recorded.

Predation risk

Counting the number of key predator species that flew within 10m of the colony during observations assessed predation risk; at this distance predators could reasonably be described as surveying the colony. Any predation events were recorded, noting predator

species, nest site targeted and the outcome (egg or chick loss). Any post predation courtship and copulation were also recorded to assess any attempts to lay again.

Permissions

The island Warden gave permission for the study to be undertaken (by email, available upon request) and in person on the island in 2015. All observers followed the code of conduct of the U.K. Association for the Study of Animal Behaviour.

Table 2: Duration of observations and weather conditions for all observers. Note that RS had access to an anemometer. This amounts to 4088 minutes (68.13 hours) of observation across 25 sessions

Observer	Date	Start time	Stop time	Weather			
				Rain	Wind speed	Wind direction	Cover (%)
TD	12/06/16	09:57	11:20	None	Light	W	100
	13/06/16	06:15	07:45	Light	Light	W	100
	14/06/16	06:20	07:42	None	Strong	W	100
	15/06/16	06:10	07:48	None	Light	W	100
KN	07/06/16	11:55	14:15	None	Still	-	20
	08/06/16	12:30	14:45	None	Slight	-	100
	09/06/16	10:55	13:35	None	Still	-	10
	10/06/16	11:15	13:30	Light	Slight	-	90
	11/06/16	14:55	15:55	None	Slight	S	0
	12/06/16	11:30	15:00	None	Slight	S	100
	13/06/16	08:00	11:10	Light/Mod.	Breezy	-	100
	14/06/16	11:35	14:00	None	Strong	N	100
	15/06/16	09:55	13:00	Light	Strong gusts	N	100
	16/06/16	08:30	09:40	None	Breezy	-	100
	17/06/16	10:45	13:50	None	Strong	-	100
RS	06/06/16	06:30	10:30	None	5 kph	SE	50
	07/06/16	06:30	11:00	None	2.8 kph	SW	100
	08/06/16	14:30	17:30	None	1.4 kph	SW	37.5
	09/06/16	06:30	10:30	None	8.6 kph	SE	12.5
	10/06/16	06:20	11:20	Light	5.4 kph	E	100
	12/06/16	06:15	10:00	Light	3 kph	SW	100
	13/06/16	11:00	13:15	Light	3.5 kph	SW	100
	14/06/16	13:55	16:45	None	17 kph	SW	87.5
	15/06/16	12:55	15:55	None	5 kph	NW	100
	16/06/16	13:00	16:00	None	1.5 kph	NW	50

RESULTS

Analysis strategy

No predations or attempted predations were witnessed during the entire study.

The raw data is presented and missing data biases analysed. The census data is described, to give a sense of colony activity, a dependent variable of clutch size for each nest is calculated. Clutch size is compared across nest characteristics and zones.

Means and standard deviations will be reported as mean (standard deviation) throughout. Inferential statistics were calculated using IBM SPSS v21 on an iMac OSX.

Raw count data

Tables 3a-c display the summarized counts of eggs and chicks for 58 nests for each observer on the project; missing data are reported. Late in the study a new nest (nest 60) was established. This was excluded from all subsequent analyses as the adults had not had time to lay. Nest 57 proved to be just a perch. Upon photographic analysis, 57 was close to an apparently abandoned nest wedged behind 15.

Table 3a: TD data: number of eggs and chicks in each category of count and total egg and chick counts for the day. Missing data also represented. N=58 nests

Date	Eggs						Chicks				
	Zero	One	Two	Three	Total eggs	Missing Data	Zero	One	Two	Total chicks	Missing Data
12/06/16	2	8	8	-	24	40	17	1	0	1	40
13/06/16	8	8	3	-	14	39	15	2	2	6	39
14/06/16	5	4	3	-	10	46	10	2	0	2	46
15/06/16	6	12	6	-	24	34	21	1	2	5	34

Table 3b: KN data: number of eggs and chicks in each category of count and total egg and chick counts for the day. Missing data also represented. N=58 nests

Date	Eggs						Chicks				
	Zero	One	Two	Three	Total eggs	Missing Data	Zero	One	Two	Total chicks	Missing Data
07/06/16	3	11	6	-	23	38	-	-	-	-	58
08/06/16	3	10	5	-	20	40	-	-	-	-	58
09/06/16	3	6	13	1	35	35	-	1	-	1	57
10/06/16	2	5	17	-	39	34	-	1	-	1	57
11/06/16	3	3	5	-	13	47	-	-	1	2	57
12/06/16	4	11	19	2	55	22	-	2	1	4	55
13/06/16	5	7	12	-	31	34	-	3	1	5	54
14/06/16	7	7	6	-	19	38	-	4	3	10	51
15/06/16	7	11	4	1	22	35	-	5	3	11	50
16/06/16	10	3	2	-	7	43	-	2	3	8	53
17/06/16	16	8	7	1	25	26	1	9	6	21	42

Table 3c: RS data: number of eggs and chicks in each category of count and total egg and chick counts for the day. Missing data also represented. N=58 nests

Date	Eggs						Chicks				
	Zero	One	Two	Three	Total eggs	Missing Data	Zero	One	Two	Total chicks	Missing Data
06/06/17	-	4	5	1	17	48	-	-	-	-	58
07/06/16	-	2	5	1	15	50	-	-	-	-	58
08/06/16	-	4	5	-	14	49	-	-	-	-	58
09/06/16	-	10	11	-	32	37	-	1	-	1	57
10/06/16	-	2	3	-	8	53	-	-	1	2	57
12/06/16	-	5	6	-	17	47	-	-	1	2	57
13/06/16	-	4	2	-	8	52	-	3	-	3	55
14/06/16	-	8	6	1	23	43	-	5	2	9	51
15/06/16	-	8	3	1	17	46	-	7	2	11	49
16/06/16	-	6	5	1	19	45	-	5	4	9	49

Missing data biases

Missing data refers to nests for which no data were collected during an observation; so a missing data value gives the number of nests for which there is no data. For each observer, the percentage of missing data was calculated for each nest over the complete study. The distribution of percentage missing data across the three observers and five zones of the colony was then analysed, in order to check for any biases in observation. The missing data were normally distributed, however a Levene's test revealed that the homogeneity of variance assumption was violated between the three observers ($F=22.27_{2,171}$; p=0.0001). To this end, a non-parametric two-tailed Kruskal-Wallis test was conducted to assess equality in the distribution of missing data across observers. The result was significant (H=10.12; df=2; p=0.006). The null hypothesis can be rejected, as the distribution of missing data was unequal across all observers. TD had the lowest mean missing data [68.10], RS the highest [85.80], with KN in the middle [77.12].

A Levene's test revealed that the homogeneity assumption was not violated for missing data across zones. Given this, a one-way ANOVA was conducted to assess the inequality in the distribution of data across zones. Data were unevenly distributed across the five zones ($F=4.91_{24,169}$; p=0.001). Post-hoc tests revealed that there were significantly more missing data from zone D.

A Fisher's Exact test was conducted to assess any association between observer and zones with regard to the recording of missing data. This was found to be non-significant, providing no evidence of observer bias in favour of particular parts of the colony.

Census data

Census data for 59 sites (including one perch) was collapsed across each complete census and across observers in order to assess AON (Bibby *et al*. 2000). The modal occupancy was 57 nests and the mean AON was 53.10 (11.77).

Clutch size variable (c_i)

Missing nest data is an issue, but so too is incomplete nest data. As contents were often only briefly and partially observable it is not possible to be certain of final counts. There was also a lot of variance in count data across observers ($F=46.73_{2,760}$; $p=0.001$). To this end all methods of calculating clutch size used measures of central tendency across the entire data set. Given the number of observations taken, and the use of more than one observer, the probability of gathering data from a significant number of nests in the colony is also increased.

Using last day data from each contributing observer a mean clutch size variable was computed for each nest (c_i), combining egg and chick counts. The last day is simply the last day an egg or chick count is recorded for a nest site. Where standard codes revealed count data, in the absence of other data, it was assumed that count referred to eggs and this was entered into the analysis, given the low number of chicks relative to eggs (Tables 3a-c).

The mean was calculated across the number of observers contributing to each nest: nests with complete data could have contributions from between 1 and 3 observers. In this way the number of nests with missing data were reduced to only three, giving data for 55 nests (94.83% of the overall observed colony).

Alternative calculation of c_i

Three mean clutch size variables for each nest were calculated, one for each observer, across all egg and chick counts, across all days. The mean of these means was then calculated, yielding one value for each nest. This reduced the missing data to only three nests. All the analyses reported below were conducted using this variable also, and the same results were found. For ease of exposition they are not reported here.

Nest characteristics

c_i was found to be normally distributed using P-P plots, and used as a dependent variable in four separate one-way ANOVAs (Table 4). Each of these analyses tested to see if clutch size varied across key nest variables: namely, zone; position (upper/lower portions of the colony); the number of neighbours within pecking distance from a sitting position; and, the number of vertical walls (Gaston & Nettleship 1981). All results were non-significant indicating an even distribution of clutch size across the colony, as defined by these variables.

Table 4: Results of four one-way ANOVAs with mean clutch size, c_i, as the dependent variable. As can be seen the zone, position, number of neighbours and number of vertical walls had no impact upon the mean clutch size. This suggests that potential productivity is potentially even across the colony, at the time of survey

	Degrees of freedom				
	Between	**Within**	**Total**	***F***	***p***
Zone	4	50	54	0.750	0.563
Position	1	53	54	0.054	0.816
Neighbours	2	52	54	0.608	0.548
Vertical	3	51	54	1.483	0.230

Pearson Chi-square tests revealed no association between the number of neighbours and position in the colony, nor between the number of neighbours and the number of vertical walls. Subsequent linear regression analyses revealed no significant interactions between these characteristics. Ledge width and the presence or absence of a roof were also recorded (Gaston & Nettleship 1981) but there was a great deal of uniformity across the colony with 54 nests on narrow ledges (4 medium) and only three with a roof. These independent variables were not analysed further.

Possible instances of egg/chick loss were calculated. Loss, for each nest, was defined as follows: where two or more counts of zero contents were recorded on the 16 and 17 June, in conjunction with three or more egg/chick counts across one or more observers at any time prior to 16 June. This set of criteria were quite stringent, but enabled consistent observations across more than one observer to be used, increasing their reliability. (There were 10 nests that had last day data of zero registered by one of the observers, so this method discounted 50% of the final zero counts.) The exact amount of loss could not be determined due to variation in the preceding data. In effect, all egg and chick registrations were simply seen as presence data, but missing data were not counted as evidence of loss; only definite zero counts.

This method yielded five potential losses: three in Zone C (nests 9, 12, 14) and two in Zone A (nests 22, 24). None of the nests had a roof, three had one vertical wall, one had two vertical walls and one had three. Three nests were on narrow ledges, and two on medium.

Comparison of 2015 and 2016 data

Data were collected for the same colony from 6-12 June 2015 (Dickins 2016). At that time there were 71 AON. (Note that AON=71 is c.28% lower than the AON=98 in Figure 2a, possibly due to overestimates introduced by only counting occupancy (Bibby *et al*. 2000).) The average clutch size was calculated as 0.933 (last day method) eggs per nest. For 2016 the average clutch size was 1.42 (last day method) with a mean AON of 53.10.

Using photographs and maps from both years, the 2015 nest codes (N=71) were translated to 2016 codes (N=58). There were 48 nests in common across both years. Perches from 2015 had become nests in 2016, and vice versa. More ledges were used for nest sites in 2015 than in 2016.

Both sets of data for the 48 common nests were normally distributed according to inspection of P-P plots. A two-tailed paired sample t-test revealed a significant difference between the two years (t=-3.62; df=32; p=0.001) with 2016 having a higher mean of 1.09 (0.91) compared with a 2015 mean of 0.45 (0.67).

The 48 common nests and their last day data were analysed for vertical wall and zone characteristics. These characteristics did not change across the two-year period, whereas the number of neighbours had. Due to the uniformity of ledge and roof structures, group sizes were too small for meaningful comparisons of difference across these categories. The 2016 data met all parametric assumptions and two one-way ANOVAs were non-significant (Table 5).

Table 5: Results of two one-way ANOVAs with 2016 mean clutch size from the common nests as the dependent variable

	Degrees of freedom				
	Between	**Within**	**Total**	***F***	***p***
Vertical	3	41	44	0.568	0.639
Zone	4	40	44	1.596	0.194

Levene's tests revealed that the 2015 data were non-parametric, therefore Kruskal-Wallis tests were performed across the vertical (H=3.21; df=3; p=0.36) and zone (H=6.94; df=35; p=0.139) categories and both were found to be non-significant. As with the 2016 data, the clutch size data were evenly distributed across all categories.

Table 6: Number of adult and juvenile loafing birds at the beginning and end of each observation period for all observers. The mean and standard deviation across all observers indicates considerable variance in the data. Discussion after the observations were conducted revealed some differences of opinion between observers about where to count loafers and this had caused some difficulty in the field. To this end there may be considerable measurement error. Nonetheless, all of these birds were loafing within sight of the colony and there are no other colonies in the immediate vicinity

		Loafing adults		Loafing juveniles	
Observer	**Date**	**Beginning**	**End**	**Beginning**	**End**
TD	12/06/16	7	20	0	0
	13/06/16	7	14	0	0
	14/06/16	19	20	0	0
	15/06/16	67	18	1	0
KN	07/06/16	4	3	0	0
	08/06/16	5	4	0	0
	09/06/16	13	7	0	0
	10/06/16	9	8	0	0
	11/06/16	5	5	0	0
	12/06/16	28	39	0	0
	13/06/16	30	16	0	0
	14/06/16	64	72	6	7
	15/06/16	30	48	3	4
	16/06/16	18	18	1	0
	17/06/16	4	26	0	4
RS	06/06/16	10	13	0	0
	07/06/16	17	16	0	0
	08/06/16	4	3	0	0
	09/06/16	4	8	0	0
	10/06/16	9	5	0	0
	12/06/16	7	9	0	0
	13/06/16	12	6	0	0
	14/06/16	20	16	0	0
	15/06/16	11	17	1	0
	16/06/16	5	5	0	0
Statistics	Mean	16.36	16.64	0.48	0.60
	Standard deviation	16.87	15.86	1.33	1.73

Other data

Data were collected on the number of loafing Kittiwakes near to and in the colony, and neighbour disputes between nesting birds (Tables 6 and 7). The number of fly-bys by predatory birds (within 10m of the colony) was recorded. There were 25 nest disputes across 25 observations; a low number. There was great variation in the number of loafers, but only a small number of juveniles in keeping with low philopatry as these birds tend to disperse. Across all observers a total of 67 Herring gulls, 11 Lesser Black-backed gulls *(Larus fuscus)*, 18 Great Black-backed gulls, two Carrion Crows *(Corvus corone)* and four Peregrine falcons flew within 10m of the colony. With 68.13 hours of observation this yields a rate of 1.497 fly-bys per hour.

Table 7: Nest disputes organized by observer, date and time of occurrence. Nests 15 and 57 had eight recorded disputes. Nest 57 was technically a perch, next to a nest wedged behind nest 15. There had been a nest more toward the perch position in 2015. The wedged nest in 2016 had an egg in it but the adult was not observed to incubate

			Causality determined		Causality undetermined	
Observer	**Date**	**Time**	**Actor**	**Recipient**	**Nest**	**Nest**
TD	13/06/16	06:50	15	57	-	-
	15/06/16	06:35	30	31	-	-
KN	07/06/16	12:35	27	31	-	-
	10/06/16	12:23	11	10	-	-
	10/06/16	12:31	23	24	-	-
	11/06/16	15:10	-	-	39	40
	11/06/16	15:40	-	-	28	29
	12/06/16	12:34	-	-	45	46
	13/06/16	08:45	23	24	-	-
	13/06/16	09:25	15	57	-	-
	14/06/16	13:25	15	57	-	-
	15/06/16	11:05	15	57	-	-
	15/06/16	11:17	-	-	39	40
	15/06/16	11:27	45	46	-	-
	15/06/16	11:40	-	-	44	47
	15/06/16	12:30	45	46	-	-
	17/06/16	13:40	57	15	-	-
RS	06/06/16	08:10	15	57	-	-
	06/06/16	09:00	57	15	-	-
	12/06/16	06:50	14	12	-	-
	12/06/16	08:00	23	24	-	-
	12/06/16	08:20	57	15	-	-
	14/06/16	14:20	44	47	-	-
	15/06/16	15:20	22	23	-	-
	16/06/16	14:45	35	36	-	-

DISCUSSION

No predation or predation attempts were observed during this study, but predators were present, indicating some predation risk. The mean clutch size for the colony was 1.42 eggs; larger than the preceding year by 0.487 eggs, suggesting better breeding conditions (Jacobsen *et al*. 1995). No significant effects of colony or nest characteristics were found in clutch size for 2016, nor for the common nests across 2015 and 2016. This suggests that risk may be evenly distributed across the colony, at least for these two years.

Limitations and future directions

The current study was time limited. Twenty-five observation periods took place over 11 days, with a mean observation period of 163.52 minutes (standard deviation=63.15) with 68.13 hours of data collected. All observations were conducted during the day. Predation attempts could easily have been missed, especially in the early evening, dusk and night when no sampling occurred. A more thorough sampling across the day is required, possibly introducing camera traps to capture nocturnal data (Collins *et al*. 2014).

Given previous observations (Dickins 2016), the predator fly-by rate and the healthier status of the colony in 2016 it is not unreasonable to assume a change in predation regime. Such a change may be attributable to shifts in abundance in other prey items (Charnov 1976) and also to changes in predator abundance. During the course of the study it was noted that rabbit abundance was very high, and that the number of rabbit carcasses around the island was also high. Upon later enquiry it was discovered that some of these carcasses had been left after deliberate control. Rabbit populations on the island have fluctuated from a high of around 15,000 individuals (Smith & Compton 2008) to a low of fewer than 200 individuals following an outbreak of myxamatosis in 2006 (Saunders 2008). The impact of rabbit activities upon the archaeology and conservation effort on the island has been seen as a problem, and it is a policy to control numbers to avoid the excesses of a 15,000 population (Saunders 2008).

Optimal foraging theory would predict that the increased rabbit abundance, and the decision to leave rabbit carcasses as available carrion, would lead to shifts in predation strategy for Great Black-backed gulls and other predators (Charnov 1976; Krebs *et al*. 1977). Effectively the ratio of search time costs to energy return from eggs is very likely less favourable than that for freely available carrion. To this end it would be of great use to collect data on rabbit and other prey abundance and relate it to Kittiwake and other seabird productivity. More generally, modelling the food web dynamics on the island would help to untangle predation risk for Kittiwakes (Abrams 2000; Abrams & Ginzburg 2000; Abrams 2010; Beckerman *et al*. 2006; Petchey *et al*. 2008).

Sand-eel availability at sea is also important. Sand-eel abundance data is not available for the Lundy Kittiwakes. It might be possible in the future to estimate annual variation from careful counts of sand-eels fed to young Kittiwakes and auk species.

The production of a last-day mean for individual nest clutch size (c_i) enabled missing data to be reduced significantly. This variable treated all observations as equal. However, we can be reasonably confident that the detectable biases in missing data between observers will be averaged out. For future study it would be wise to assess observers over a time limited survey of the same site and check to see how many eggs they detect and

how many of those eggs are in common nests (Gaston & Nettleship 1981). It would also be good practice to have consistent time periods for observations across observers, in order to equalize survey effort and standardize.

Ideally the colony would be followed throughout the entire breeding season for at least one year to assess how useful June count data are. This would also assay any changes in risk profile across the year. Related to this, information about predator phenology would be useful, in the context of general prey abundance. It is assumed that predators time their own reproductive effort to match peak productivity in their prey (Lack 1950). At present the phenology of Great Black-backed gulls, and other predators on the island is not monitored. It is possible that Great Black-backed gull and Kittiwake breeding was asynchronous this season. The lack of specialism in Great Black-backed gulls will also introduce variance as they pursue different prey items according to abundance.

Conclusion

Two seasons of average clutch size data have been collected for this colony, whilst productivity has been surveyed for longer. Productivity has been measured in relation to AON counts, which is not as precise as direct count methods. With longer-term data it will be possible to work out more accurate percentage success and loss and to develop a richer picture of Kittiwake reproductive decisions in this southern population.

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